SURVIVAL ESTIMATES FOR FLORIDA MANATEES FROM THE PHOTO-IDENTIFICATION OF INDIVIDUALS

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Abstract

We estimated adult survival probabilities for the endangered Florida manatee (*Trichechus manatus latirostris*) in four regional populations using photo-identification data and open-population capture-recapture statistical models. The mean annual adult survival probability over the most recent 10-yr period of available estimates was as follows: Northwest – 0.956 (SE 0.007), Upper St. Johns River – 0.960 (0.011), Atlantic Coast – 0.937 (0.008), and Southwest – 0.908 (0.019). Estimates of temporal variance independent of sampling error, calculated from the survival estimates, indicated constant survival in the Upper St. Johns River, true temporal variability in the Northwest and Atlantic Coast, and large sampling variability obscuring estimates for the Southwest. Calf and subadult survival probabilities were estimated for the Upper St. Johns River from the only available data for known-aged individuals: 0.810 (95% CI 0.727–0.873) for 1st year calves, 0.915 (0.827–0.960) for 2nd year calves, and 0.969 (0.946–0.982) for manatee 3 yr or older. These estimates of survival probabilities and temporal variance, in conjunction with estimates of reproduction probabilities from photo-identification data can be used to model manatee population dynamics, estimate population growth rates, and provide an integrated measure of regional status.

Key words: survival probabilities, capture-recapture, *Trichechus manatus latirostris*, manatee, photo-identification, sighting probabilities, temporal variance, Program MARK.

Assessment of survival rates and the factors that affect survival are central to our understanding of large mammal population dynamics. It has been demonstrated for various species, including marine mammals (Eberhardt and Siniff 1977, Eberhardt 1985) and manatees (Eberhardt and O'Shea 1995, Runge *et al.* 2004) that population growth rates are most sensitive to changes in adult survival probability. Nonetheless, juvenile survival probabilities of large mammals in general are more sensitive to environmental variation than are adult survival rates (Eberhardt 1977, Benton and Grant 1996) and can show high annual fluctuations (Gaillard *et al.* 1998). Variation in age-specific survival of immatures can play an important role in determining population fluctuations and trend (Eberhardt and Siniff 1977, Gaillard *et al.* 1998).

Accurate assessments of age-specific and population-specific survival, temporal variability, and the identification of the factors affecting variability are important for the management and conservation of marine mammals (Fujiwara and Caswell 2001, Zeh *et al.* 2002), and particularly for the endangered Florida manatee (*Trichechus manatus latirostris*). Currently, we lack robust statistical means to directly estimate and monitor trends in manatee population size and growth rate using the current aerial survey methods (directly counting manatees at winter aggregation sites; Lefebvre *et al.* 1995). However, robust methods are available to monitor known, individual manatees with photo-identification (Beck and Reid 1995), to estimate survival rates with open-population capture-recapture statistical models, and to model and test hypotheses regarding patterns of variation in survival and the natural or anthropogenic factors affecting that variation (O'Shea and Langtimm 1995, Langtimm *et al.* 1998, Langtimm and Beck 2003). These estimates can then be integrated with other life-history parameters to model population dynamics and population growth rate (Eberhardt and O'Shea 1995, Runge *et al.* 2004). Population models incorporating parameters estimated from the sightings of live individuals are being developed by federal and state management agencies to assess status and recovery of the species under the U.S. Endangered Species Act (USFWS 2001) and the Florida Endangered and Threatened Species Act of 1977 (FMRI 2002),[1] and to determine acceptable levels of incidental take from watercraft collisions under the Marine Mammal Protection Act (USFWS 2002).

Capture-recapture survival models were first applied to manatee photo-identification data in the 1990s (O'Shea and Langtimm 1995, Langtimm *et al.* 1998) for three of the four regional subpopulations in the state of Florida (Fig. 1) recognized as management regions in the latest revision of the Florida Manatee Recovery Plan (USFWS 2001). Since then, the Manatee Individual Photo-identification System (MIPS) has developed into a multi-agency collaboration to annually photo-document individually recognizable manatees throughout Florida. Here we present the first adult survival estimates for the Southwest region, and

[1] Florida Marine Research Institute [FMRI]. 2002. Final biological status review of the Florida manatee (*Trichechus manatus latirostris*), December 2002. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg, FL.
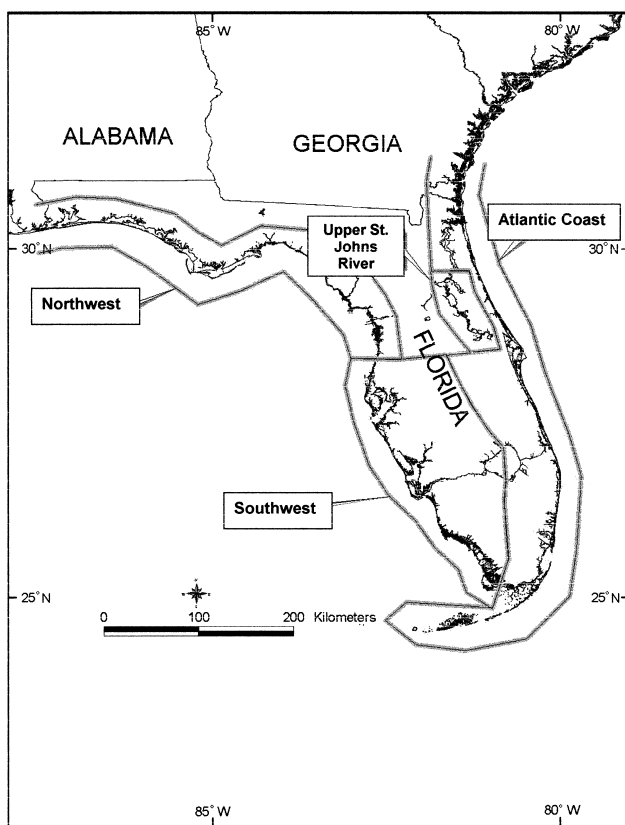
Figure 1. Map of the geographic locations of the four subpopulations in Florida.

updated estimates for the other three regions (Northwest, Upper St. Johns River, and Atlantic Coast). We examine patterns of variation in manatee survival probabilities and provide the first estimates of temporal variance, independent of sampling error as required for population models that incorporate environmental stochasticity in demographic parameters (*e.g.*, population viability analysis). Finally we present recommendations for improving data collection and survival analysis proposed by a review panel to the Manatee Population Ecology and Management Workshop held in Gainesville, Florida, April 2002. We anticipate that approaches identified to contend with several manatee issues (*e.g.*, temporary emigration from the study area, known deaths, and incidental observations of individuals between formal sampling periods) will be germane to other marine mammal resighting studies.

METHODS

The Manatee Individual Photo-identification System

In 1988 researchers developed a computer-based cataloging system to manage photo-identification data collected in the long-term study of manatee life history

Figure 2.   Example of the scars used to identify individual manatees.

traits (Beck and Reid 1995). In winter, manatees aggregate at natural and artificial warm-water sites throughout coastal Florida. These aggregations can number in the hundreds of individuals at some sites, affording non-intrusive opportunities to observe and photograph distinct individuals that can be identified by naturally occurring marks and scars. Photo-identification based on natural marks is a common approach used to study the life history of marine mammals (see Hammond *et al.* 1990). The approach for Florida manatees, however, is based primarily on animals being injured and scarred by collisions with watercraft (Fig. 2), rather than on the use of natural patterns in pigmentation, fin and fluke shape, or callosities of the dermis used with other marine mammals. Natural marks such as medial-tail notches or congenital deformities do occur, but often are indistinct for reliable individual recognition (Beck and Reid 1995). Thus calves (1- and 2 yr of age) have few distinct marks, making it difficult to monitor known-age individuals. A technique developed by photographers to clip dermal notches from the tail margin of free-swimming calves, however, has proved successful at some monitoring sites to assist in the future identification of returning calves and subadults.

Further development of the computerized catalog resulted in a system identified as MIPS, the Manatee Individual Photo-identification System. MIPS, with its criteria for cataloging individuals, its protocols for photo-documentation, and its computer-aided search protocols to assist researchers in making matches, have been designed to deal with the dynamic nature of the identifying marks (Beck and Reid 1995). Only healed scars or natural features that are unique and easily recognized are used for identification. An injury from a single encounter with watercraft often is all that is needed to provide one or several unique identifying marks, which would qualify an individual for cataloging in MIPS. However, nearly all individuals in the catalog have multiple scar patterns distributed over more than one part of the body, which provide redundant information to determine and verify identities. Before an animal is cataloged there has to be complete photographic documentation of the dorsal and lateral views of the body and tail, including those parts without scars, to ensure that the candidate has not been previously cataloged. Positive matches require verification from at least two experienced personnel, one being the database manager. Documentation of newly acquired scars or changes in marking patterns is facilitated by the high return rate of individual manatees each year to the monitored sites and consistent monitoring of these sites by experienced observers.

The Four Regions and Photo-identification Monitoring

The four regions identified as management units in the Florida Manatee Recovery Plan (USFWS 2001) differ in habitat, population attributes, and photo-identification efforts. The subpopulation in each region is composed of individuals that tend to return to the same warm-water refuges each winter and have similar non-winter distribution patterns. Exchange of individuals among regions is considered to be limited, based on data from telemetry (Rathbun *et al.* 1990, Reid *et al.* 1991, Weigle *et al.* 2001, Deutsch *et al.* 2003) and photo-identification (CAB unpublished). Genetic differentiation has been documented between the Gulf and Atlantic coasts, but not within coasts (Garcia-Rodriguez 2000) indicating gene flow among regions. Aerial surveys show differences in the counts of individuals for each region (Ackerman 1995). There are also regional differences in human population, development, implementation of conservation and management actions, habitat characteristics, habitat quality, and factors affecting carrying capacity. Mortality risks differ not only in the magnitude of human interactions, particularly with watercraft (O'Shea *et al.* 1985, Ackerman *et al.* 1995), but also in the frequency of natural events such as cold stress (Buergelt *et al.* 1984), red-tide epizootics (O'Shea *et al.* 1991, Bossart *et al.* 1998), and hurricanes (Langtimm and Beck 2003).

The Northwest and Upper St. Johns River regions (Fig. 1) contain the two smallest subpopulations. The Upper St. Johns River is roughly calculated to contain only 4% of the Florida population, with approximately 12% in the Northwest (USFWS 2001). The winter aggregations in both regions have been the focus of research based on monitoring marked individuals since the 1970s (Hartman 1979; Rathbun *et al.* 1995, O'Shea and Hartley 1995). Manatees in the regions are the least impacted by human interactions and development. The major winter refuges are at natural, warm-water springs in the headwaters of the Crystal and Homosassa rivers in the Northwest and at Blue Spring, Volusia County, in the Upper St. Johns River. Large areas of undeveloped summer range habitat still remain. Both regions have a strong history of enforced protection efforts at the winter aggregation sites and the number of recovered carcasses has been low over the years (Ackerman *et al.* 1995). The Northwest, however, has experienced multiple hurricanes and winter storms of Category 3 or greater intensity with correlated effects on adult survival probabilities (Langtimm and Beck 2003). Clear spring-fed waters afford excellent underwater and surface photography for identification of individuals. The sex of most individuals can be determined by visual observation by underwater photographers of the position of the urogenital slit.

Data for the Upper St. Johns River have been a nearly complete annual census over the last 20 yr (O'Shea and Hartley 1995). The small aggregation in the small run at the primary site at Blue Spring State Park allowed a single observer (WCH) viewing animals from a canoe to identify individuals almost daily during winter. Because of intense monitoring, close approach, and familiarity with the animals, more subtle features can be used to identify individuals, including calves and sub-adults, than is possible at other sites. Dermal notches taken from various positions on the margin of the tail of unscarred calves help to identify returning 2nd-yr calves and subadults. This is the only region with adequate data to estimate survival of calves and subadults from known-age individuals.

In contrast, the Atlantic Coast and the Southwest regions (Fig. 1) contain the two subpopulations with the greatest impact from human interactions and development and the largest counts during aerial surveys. USFWS (2001) estimates

that the Atlantic Coast contains 47% of the Florida population, while the Southwest contains 37%. The major winter aggregation sites are industrial warm-water effluents, primarily at aging coastal power plants. The primary sites on the Atlantic Coast from north to south are in Brevard County, and at Riviera Beach, Fort Lauderdale, and Miami. The primary monitoring sites in the Southwest are in areas of Tampa Bay, Charlotte Harbor, and the city of Ft. Myers; Sarasota Bay is primarily monitored in summer rather than winter. The summer range in both regions is in some of the most heavily developed areas of the state. County protection plans have had a checkered history of implementation (USFWS 2001). Cold-stress mortality is a concern throughout the state, but carcass recovery data indicate that when cold events occur, the northeastern Atlantic Coast and the Southwest region have the highest numbers of mortalities (Ackerman *et al.* 1995). Mortality from red-tide events has only been documented in the Southwest (O'Shea *et al.* 1991, Bossart *et al.* 1998).

Photo-identification conditions are often difficult for both the Atlantic Coast and Southwest regions. Photographs are usually of manatees at or near the surface taken either from shore or a boat. Dark, turbid water is a problem, particularly for the Southwest. Because of the difficult viewing conditions, consistent monitoring in these regions occurred several years after monitoring began in the Northwest and Upper St. Johns River. There are fewer years of data on the Atlantic Coast (Reid *et al.* 1991) and in the Southwest and identification of sex is not available for all cataloged animals. Farther south on both coasts, where temperatures are warmer, individuals converge on the winter aggregations only during brief bouts of cold weather, limiting the sampling window during years with warmer winters. Few data are available for animals in south Florida near Everglades National Park and the Florida Keys.

Construction of Sighting Histories

Manatees are photographed at all times of the year, but for the Upper St. Johns River, Atlantic Coast, and Southwest analyses we defined a sample interval of 90 d when manatees were clustered and most readily photographed at the winter sites. The starting date for sampling varied by region; cold temperatures drive manatees to the winter refuges earlier in the season for the Northwest and Upper St. Johns River than for the Southwest and Atlantic Coast. Photographing manatees is time-consuming and weather dependent, and a 3-mo interval was required to obtain adequate sample sizes. Generally, in capture-recapture analysis, the assumption of equal probability of survival among individuals requires the sample interval to be negligible compared to the interval between samples (Pollock *et al.* 1990:18–19). Survival probabilities are estimated for the time between samples. However when daily mortality probabilities are low, as is the case for manatees, the expected bias from the longer sampling interval should be small (Hargrove and Borland 1994). Expanding the sampling interval beyond 90 d, particularly for the more southern sites, could introduce heterogeneity in capture probabilities, a violation of the assumption of equal probability of capture. Manatees show distinct differences in their winter and summer ranges (Deutsch *et al.* 2003). If the sample interval is too broad, individuals traveling through the area to their winter or summer range do not have the same probability of resighting the following year as individuals that over-winter at the site. Nonetheless, for the Northwest analysis we used a sample interval of 120 d in order to compare our estimates to those of an earlier published

analysis on storm effects (Langtimm and Beck 2003). This is the northernmost primary aggregation site in Florida, with the longest winter season, and the goodness of fit (GOF) test (see below) did not detect any substantial heterogeneity.

As noted by Caswell *et al.* (1999) for the North Atlantic right whale, if a major sampling area is no longer regularly sampled, individuals with high fidelity to the area have lower probabilities of being sighted in other areas and estimates may be biased low after changes to the monitoring regime. Capture-recapture techniques, based on the sighting of live individuals, estimate the apparent survival and cannot differentiate between dead animals and animals alive but not seen because of changes in sampling protocols or permanent emigration of individuals out of the study area. Manatee monitoring at the major aggregation sites in all regions has occurred yearly, with the exception of Ft. Pierce on the Atlantic Coast. The industrial warm-water effluent at this site was used by manatees as a temporary refuge as they traversed between Brevard County and Pt. Everglades/Miami aggregation sites (Deutsch *et al.* 2003), but the reduced operation in 1997. For this analysis, we excluded all sightings at Ft. Pierce even though the majority of animals have been sighted at other sites since the modification of the power plant (CAL, unpublished data). Permanent emigration of individuals to another region is not likely to occur on the Atlantic Coast. The primary aggregation sites used by manatees (Deutsch *et al.* 2003) are the sites used for monitoring with photo-identification. Permanent emigration is more likely in the Northwest and Southwest, but to date only a few animals have been photo-documented in both regions (CAB and KJF unpublished data) and we did not include sightings outside of a region in the data used to construct the sighting histories.

For three of the regions in the adult analysis, we further divided the sighting histories into two groups that we suspected were (1) similar in their behavior patterns, and thus equal in their probability of capture, and (2) subject to similar mortality risks, and thus equal in their probability of survival. This should reduce heterogeneity in capture and survival probabilities to better meet the assumptions of the analysis. It also affords the opportunity to examine possible factors hypothesized to affect capture and survival. For the Northwest, the groups were males and females. In addition to possible differences due to reproduction effects, radio-telemetry has documented differences between adult males and females in warm-season movement patterns (Deutsch *et al.* 2003). Males have higher daily travel rates and spend more time away from their core warm-season range. For the Upper St. Johns River, the groups were based on probable recruitment into the population—those first sighted as a 1st-yr calf at the aggregation site (*i.e.*, "native born" to the region) and those first sighted as a subadult or adult. This last group contained individuals of unknown origin, either native to the Upper St. Johns River, but more probably migrants from the Lower St. Johns River and the Atlantic Coast. Sightings as a calf were excluded from the analysis. Analysis of telemetry data has documented natal philopatry of offspring to migratory patterns learned from mothers during the 1.5–2.0-yr dependent period (Deutsch *et al.* 2003). Thus one might expect differences in winter site fidelity between "natives" and "immigrants" and thus differences in capture probability. In the Southwest, we divided the sightings into a northern segment in Tampa Bay and a southern segment at Charlotte Harbor and Ft. Myers. Sightings in the region of Sarasota Bay, between the north and south locations, were excluded from the analysis because the area is monitored primarily in summer. Manatee deaths from red tide periodically affect the region (O'Shea *et al.* 1991). The last major event included in this analysis

Table 1. Summary of the data sets for each of the four regions.

Region	Time span of data[a]	Number of years of data	Number of individuals
Northwest	1981/82–2000/01	20	342
Upper St. Johns River	1979/80–2000/01	22	197
Atlantic Coast	1984/85–2000/01	17	660
Southwest	1994/95–2001/02	8	361

[a] Sample interval begins at the end of one year and finishes in the next.

was in 1996, with higher numbers of carcasses recovered in the south (Bossart *et al.* 1998). Comparison of the individual sighting histories for the two groups showed that only 5 of 361 individuals were sighted in both groups over the 8-yr study, suggesting only a small exchange of individuals between the north and south segments, at least in winter. We were not able to divide sightings on the Atlantic Coast into segments. Telemetry (Deutsch *et al.* 2003) and photo-identification (CAL unpublished data) have documented individual and annual variation in winter migration patterns along the coast; a few manatees are year-round residents to the central part of the coast while a large number migrate and are tracked or sighted at several aggregations sites within a winter season.

For analysis of adult survival rates, sightings of individuals were included only after they became adults (>5 yr), following the criteria defined by O'Shea and Langtimm (1995). This age threshold ensures valid estimates of adult survival as it excludes the earliest known ages of sexual maturity (Hernandez *et al.* 1995, Marmontel 1995, O'Shea and Hartley 1995, Rathbun *et al*. 1995). For analysis of calf and subadult survival rates, only sightings of individuals known from their first or second year as a calf were included. Each sighting history consisted of the sighting (1) or non-sighting (0) of the individual at least once during the winter samples for each year of the study. A full discussion of the criteria for constructing the manatee sighting histories to meet the assumptions of capture-recapture analysis was given in Langtimm *et al.* (1998). A summary of the final data sets is presented in Table 1.

Capture-Recapture Modeling Procedures

We used Program MARK (White and Burnham 1999) to model variation in adult survival and sighting probabilities for each region and to estimate these probabilities under the various models. Our modeling approach followed that outlined by Lebreton *et al.* (1992). We started with the general Cormack-Jolly-Seber model (ϕ_{g*t}, p_{g*t}) [notation for models follows Lebreton *et al.* 1992], allowing survival (ϕ) and sighting probabilities (p) to vary by group (g) as well as annually (t). We assessed the goodness-of-fit (GOF) of the data to this general model using Program RELEASE (Burnham *et al.* 1987), available within Program MARK. We constructed additional models based on *a priori* hypotheses about variation in survival and sighting probabilities. A summary of the factors modeled for each of the four regions is presented in Table 2.

For each region we chose the best model among those constructed using Akaike's Information Criteria adjusted for small sample size (AICc, Burnham and Anderson 1998). AICc is an information-theoretic criterion that assists the researcher in

Table 2.   Factors modeled as effects on variation in survival and detection in each region.

Factor			Northwest	Upper St. Johns River	Atlantic Coast	Southwest
Survival	Time	Year (annual)	X	X	X	X
		Year (linear)	X		X	
		Storm	X			
	Group	Sex	X			
		Native born		X		
		North/South				X
	Interaction	Group by year	X	X		X
	Additive effects	Group and year	X	X		X
Detection	Time	Year (annual)	X	X	X	X
	Group	Sex	X			
		Native born		X		
		North/South				X
	Interactions	Group by year	X	X		X
	Additive effects	Group and year	X	X		X

identifying the most parsimonious models with enough parameters to account for the structure of the data without over-parameterization and loss of precision (Burnham and Anderson 1998). Lower AICc values indicate a more parsimonious model. A variance inflation factor ($\hat{c}$) was calculated from the GOF chi-square statistic and the degrees of freedom (χ^2/df) to account for lack of fit. We used the quasi-likelihood modification of AICc (QAICc, Anderson *et al.* 1998) in model selection for data with $\hat{c}$ values greater than 1.

A lack of fit indicated violations of the assumption of equal probability of capture and survival of the marked animals in the population. This is common in biological studies of this kind due either to heterogeneity (*i.e.*, differences) in survival or capture probabilities among individuals or lack of independent sampling of individuals. Lack of independence should not be a problem with the Florida manatee. They do not form stable social groups as adults (Hartman 1979), as is the case with some cetacean species (Shane and McSweeney 1990, Wells 1991, Würsig *et al.* 1991). Movements to and from the winter aggregation sites are independent among adults (Bengtson 1981, Deutsch 2003). However, based on what we know about manatee biology, heterogeneity in survival and capture probabilities among individuals should be expected due to documented individual variation in behavior and movement patterns (Deutsch 2003) and annual variation in cold fronts and winter severity, which affect how frequently and how long manatees visit the warm-water monitoring sites during a given winter (Hartman 1979, Reynolds and Wilcox 1994, Deutsch 2003). Heterogeneity in sighting probability can also be introduced by heterogeneity in sampling (Pollock *et al.* 1990). The intensity of visits has varied over the years due to weather, funding, and logistics. Ideally this variation in capture probabilities could be modeled with an index of person-hours spent by photographers at each site, but was not available in this retrospective analysis.

Nonetheless, violation of the assumption does not negate a capture-recapture analysis. Survival estimates, in contrast to estimates of abundance, are generally

robust to such heterogeneity (Pollock *et al.* 1990) and should be subject to little bias if $\hat{c}$ does not exceed 4 (Anderson *et al.* 1994, Burnham and Anderson 1998). Precision, however, will be over-estimated, and to account for this, the variance inflation factor was incorporated into the modeling and inference methods to better reflect the larger uncertainty in precision (for a discussion see Burnham and Anderson 1998:52–53).

We used normalized Akaike weights to evaluate the expected likelihood of a given model relative to all the other models we constructed for each region (Burnham and Anderson 1998). The best model was used to obtain maximum-likelihood estimates of survival probabilities, sighting probabilities, and approximate 95% confidence intervals (95% CI).

We estimated survival for calves and subadults in the Upper St. Johns River, the only region where 1st-yr calves could be reliably resighted in subsequent years ($n = 115$). Using Program MARK, age models were constructed with specific age classes defined by the period of years since first sighting. Following O'Shea and Langtimm (1995), the initial general model included six age classes: 1st-yr calf (yr 1 of capture history), 2nd-yr calf (yr 2), three subadult classes (yr 3, 4, and 5), and adults ($>$yr 5). We then built subsequent models by pooling those age classes we suspected to experience similar survival rates, (such as all calves: yr 1 and 2; all subadults: yr 3, 4, and 5; a combination of subadults and adults: yr 5 and $>$5). Model selection procedures described above were used to select the best models to describe the data and to estimate survival probabilities for the age classes.

We also estimated temporal variation for use in models of manatee population dynamics. Models that incorporate environmental stochasticity in demographic parameters, such as population viability analysis, require estimates of temporal variance, independent of estimates of variability due to measurement error (Boyce 2001). Failure to separate this sampling variance from temporal variance can bias model results (Link and Nichols 1994, Gould and Nichols 1998). We used the variance components feature in Program MARK (White *et al.* 2001) to estimate mean survival rate and temporal variance (σ^2) for each region. The procedure in MARK is an extension of the procedure described in Burnham *et al.* (1987). Estimates were made using the lowest AICc or QAICc model where survival probabilities, but not necessarily sighting probabilities, varied annually. The calculated variance inflation factor was used in the estimation procedure. Data from all available years were used to estimate survival and variance, but the mean was stipulated to include only the most recent 10 yr of estimates in order to facilitate comparisons among regions.

<div align="center">RESULTS</div>

The results of the GOF tests (Table 3) identified a good fit of the data to the initial general model for the Northwest, but a significant lack of fit for the other three regions ($P < 0.05$). However, the variance inflation factors calculated for the Upper St. Johns River, the Atlantic Coast, and the Southwest regions were less than 4 indicating that estimates of survival should be subject to small bias from the lack of fit (Anderson *et al.* 1994, Burnham and Anderson 1998). For these regions, model selection procedures and calculation of 95% confidence intervals were modified to incorporate the appropriate variance inflation factor (Table 3) to better reflect the lower precision of the estimates.

Mean annual sighting rates were greater than 0.49 in all four regions (Table 4). Results of the model selection procedures indicated the best models included

Table 3.   Summary of the results of the goodness-of-fit (GOF) tests of the data to the general model. The variance inflation factor ($\hat{c}$) is calculated from the GOF chi-square statistic and the degrees of freedom (χ^2/df).

Region	χ^2	df	Probability level	$\hat{c}$
Northwest	121.3	126	0.602	1.000[a]
Upper St. Johns River	91.0	34	<0.001	2.370
Atlantic Coast	167.6	86	<0.001	1.949
Southwest	163.1	69	<0.001	2.676

[a] Actual estimate = 0.963, but because $\hat{c}$ <1, rounded to 1.0 following White *et al.* (2001:376).

annual variation in sighting probabilities for the Northwest and Atlantic Coast regions, with negligible annual variation for the Upper St. Johns River and the Southwest. Daily monitoring of the small number of over-wintering individuals at Blue Spring, the primary aggregation site in the Upper St. Johns River, along with strong site fidelity, accounted for the lack of variation in sighting rates for this region. The lack of detectable variation for the Southwest could be due to strong site fidelity, small samples of individuals, or the short time-series.

Evaluation of the likelihood of the various models constructed for each region provided evidence for specific temporal and ecological patterns in survival probabilities. In the Northwest, two models describing patterns of variation in survival during years with intense coastal storms ranked higher than any of the other models (AICc weight = 0.533 and 0.370 compared to 0.066 for the third ranked model). The models we fitted to the data are presented in Table 5. The highest-ranked model was one in which survival was constant over the 20-yr study with the exception of three years when intense hurricanes and a major winter storm hit the region. This storm effect, during years with Category 3 or stronger storms on the Saffir-Simpson scale (Williams and Duedall 1997), was first identified in a previous analysis with fewer years of data (Langtimm and Beck 2003). The survival probabilities estimated under this model are presented in Table 6. The second-ranked model described an additive effect of storm and sex [ϕf(storm + sex)]. The model describing the interaction between storm and sex [ϕf(storm × sex)] had poor support relative to the other storm models (AICc weight = 0.018). The AICc values for the top two models were very similar with a difference of only 0.73, indicating support for both models, but the additive effect due to sex was not significant (Likelihood ratio test, $\chi^2 = 1.314$, df = 1, $P = 0.252$). The magnitude of the difference in survival between sexes under the additive model was small at 0.01, with male survival only slightly lower than females during normal and storm years. The model describing a linear time-trend in survival probabilities was ranked third

Table 4.   Mean annual sighting probabilities (p) estimated for each region.

Region	Model[a]	p	Standard error
Northwest	$\phi_t p_t$	0.666	0.036
Upper St. Johns River	$\phi_t p_t$	0.927	0.014
Atlantic Coast	$\phi_t p_t$	0.491	0.028
Southwest	$\phi_t p_t$	0.673	0.030

[a] ϕ_t = survival probability varies by time, p_t = capture probability varies by time.

Table 5. Comparison of fit for models of survival of adults in the Northwest region.

Model[a]	# Parameters	ΔAICc	AICc weight
ϕ *f*(storm) $p(t)$	23	0.00	0.533
ϕ *f*(storm+sex) $p(t)$	24	0.73	0.370
ϕ *f*(linear trend) $p(t)$	21	4.19	0.066
ϕ *f*(storm*sex) $p(t)$	27	6.80	0.018
$\phi(\cdot)\,p(t)$	20	8.93	0.006
$\phi(g)\,p(t)$	21	9.56	0.005
$\phi(\cdot)\,p(g+t)$	21	10.86	0.002
$\phi(g+t)\,p(t)$	29	21.49	<0.001
$\phi(t)\,p(t)$	38	25.15	<0.001
$\phi(g*t)\,p(t)$	56	41.89	<0.001
$\phi(g*t)\,p(g*t)$	74	64.34	<0.001
$\phi(g)\,p(\cdot)$	3	262.35	<0.001
$\phi(g*t)\,p(\cdot)$	39	268.18	<0.001
$\phi(g*t)\,p(g)$	40	270.24	<0.001

[a] ϕ = survival probability, p = capture probability, symbols in ( ) indicate factors affecting variation, t = time, g = group, * indicates interaction, + indicates additive effect, $(\cdot)$ = no variation.

with a model likelihood of only 0.123. This was a significant negative trend when compared to the model with constant survival over time (Likelihood ratio test, $\chi^2 = 6.776$, df = 1, $P = 0.009$). Two of the major storm years with lower survival occurred during the later part of the study and would contribute to a downward trend.

The Upper St. Johns River is the only region with data of known-age animals from which to estimate calf and subadult survival ($n = 115$). The models we included in this analysis are presented in Table 7. The best model was one that included only three age-classes with different survival probabilities: 1st-yr calves, 2nd-yr calves and a single adult class consisting of yr 3 and above. There was a significant difference in survival between 1st- and 2nd-yr calves (Likelihood ratio test, $\chi^2 = 4.034$, df = 1, $P = 0.045$), but subadults at 3, 4, or 5 yr of age were not differentiated from older adults with regard to survival probability (Likelihood ratio test, $\chi^2 = 0.392$, df = 1, $P = 0.531$). The estimated annual age-specific survival probabilities were 0.810 for 1st-yr calves (0.727–0.873), 0.915 for 2nd-yr calves (0.827–0.960), and 0.969 for yr 3 and above (95% CI 0.946–0.982). The next two best models contained a subadult age-class, but differed in the number of years for subadult status. In one model, yr 3–5 were pooled into one estimate for subadults, the other model considered only yr 3 as subadult. There was very little difference between the estimates for these two age classes under either model: 0.96 for subadults and 0.97 for adults.

We estimated adult survival rates in the Upper St. Johns River from both known-age animals and the general population. Based on the lack of differences in survival probabilities for subadults and adults, we included sightings of subadults in the analysis. Relaxing the criteria for adult status increased the sample size for this relatively small subpopulation ($n = 198$). For the general model we divided the sample into two groups based on probable recruitment into the population—those first sighted as a 1st-yr calf at the aggregation site (*i.e.*, "native born" to the region, $n = 76$) and those of unknown origin who were first sighted as a subadult or adult

Table 6. Estimates of annual survival probabilities for the Northwest region under the storm covariate model ($\phi_{storm}\ p_t$).

Years	Major storms (Category 3 or 4)[a]	Lesser storms	Estimate of survival	95% confidence interval
1982–1984	0	0	0.970	0.960–0.978
1985	Hurricanes Elena and Kate	1	0.939	0.862–0.974
1986–1992	0	6	0.970	0.960–0.978
1993	"Storm of the Century"	0	0.921	0.853–0.959
1994	0	2	0.970	0.960–0.978
1995	Hurricane Opal	3	0.876	0.804–0.924
1996–2000	0	4	0.970	0.960–0.978

[a] Categories based on the Saffir-Simpson Scale (Williams and Duedall 1997).

($n = 198$). The models fitted to the data are presented in Table 8. The best model (QAICc weight=0.628) was one in which sighting probabilities differed between the two groups, but survival probability was constant over the years with no difference between groups. Annual sighting probabilities under this model were high for "natives" (0.974, 95% CI 0.932–0.970) and lower for those of unknown origin (0.845, 0.802–0.881). The estimate of survival was 0.955 (0.934–0.990). The next best model (QAICc=0.372) was one in which survival again was constant over time, but survival differed between groups. Estimates of survival probabilities under this model were 0.968 (0.927–0.987) for "natives" and 0.949 (0.921–0.968) for those with an unknown origin. The remaining models had negligible QAICc weights.

The models we fitted to the Atlantic Coast sighting histories are presented in Table 9. The model with a linear temporal trend in survival probabilities was ranked highest (QAICc weight = 0.824). The slope of the trend was negative and significantly different from a slope of zero (Likelihood ratio test $\chi^2 = 5.133$, df $= 1$, $P = 0.024$). This result however most likely is biased due to known problems with data collection during the last three years and an effect from temporary emigration (see Discussion). The second-ranked model (QAICc weight = 0.174), was one in which survival was constant over the years. The estimate of survival under this model was 0.940 (0.927–0.950).

The models fitted to the sighting histories from animals in the Southwest population are presented in Table 10. Joint modeling of the north and south segments of the population demonstrated no differences in survival probabilities between groups. The two best models were those in which survival probabilities were constant among years and equal for the groups, with sighting probabilities constant and equal (QAICc weight=0.472) or constant and different for both groups (QAICc weight = 0.202). The estimated survival probabilities under the two models were 0.903 (0.862–0.932) and 0.902 (0.862–0.932), respectively. A model with constant but different survival probabilities between groups ranked third, but the magnitude of the difference in the point estimates between the two was small: 0.895 (0.831–0.937) for the north segment and 0.909 (0.854–0.944) for the south.

Temporal variance of adult survival for all four regions was estimated for input into new models of population dynamics (FMRI 2002,[2] USFWS 2002). Survival

Table 7. Comparison of fit for models of survival of known age classes in the Upper St. Johns River region.

Model[a]	# Parameters	ΔAICc	AICc weight
$\phi_{c(1)}\phi_{c(2)}\phi_{A(>2)}\,p(\cdot)$	4	0.00	0.412
$\phi_{c(1)}\phi_{c(2)}\phi_{SA(3,4,5)}\phi_{A(>5)}\,p(\cdot)$	5	1.64	0.182
$\phi_{c(1)}\phi_{c(2)}\phi_{SA(3)}\phi_{A(>3)}\,p(\cdot)$	5	1.89	0.160
$\phi_{c(1,2)}\phi_{A(>2)}\,p(\cdot)$	3	2.01	0.151
$\phi_{c(1)}\phi_{c(2)}\phi_{SA(3)}\phi_{SA(4)}\phi_{A(>4)}\,p(\cdot)$	6	3.56	0.069
$\phi_{c(1)}\phi_{c(2)}\phi_{SA(3)}\phi_{SA(4)}\phi_{SA(5)}\phi_{A(>5)}\,p(\cdot)$	7	5.60	0.025
$\phi_{c(1)}\phi_{c(2)}\phi_{SA(3)}\phi_{SA(4)}\phi_{SA(5)}\phi_{A(>5)}\,p(\text{age})$	12	12.99	<0.001

[a] ϕ = survival probability, c = calf, SA = subadult, A = adult, numbers in parentheses = year of life included in the age class, p(age) = capture probability varied by age, p($\cdot$) = capture probability constant among age classes.

was allowed to vary annually and a mean was calculated under the variance components feature in Program MARK. The mean annual survival rate and its SE (containing both process and sample variance components) for the most recent 10-yr period are listed in Table 11 for each region (only six years of estimates available for the Southwest). The mean survival probabilities are comparable to the survival rates estimated under the best models identified in the analyses described above.

Estimates of temporal variability, independent of sampling error, are presented in Table 11 as well. Only the Northwest and the Atlantic Coast sighting data produced positive estimates of temporal variance (σ^2); the Upper St. Johns River and the Southwest were negative. Negative estimates are common in the statistical literature and have been interpreted by Gould and Nichols (1998) as indicative of temporal variation that is close to zero or not easily estimated when sampling variation is large relative to the true temporal variability. Annual sighting probabilities in the Upper St. Johns River have been very high, over 90% (Table 4) indicating that we have very good estimates of annual survival probabilities. The 95% CI for the variance estimates are narrow as well (Table 11), supporting an interpretation that temporal variation in the Upper St. Johns River is negligible and best estimated with a standard deviation (σ) of 0. In contrast, sighting probabilities in the Southwest are lower at 66% (Table 4), the results of the GOF test and variance inflation factor (Table 3) indicate heterogeneity among individuals in capture and survival probabilities, and the 95% CI for the temporal variance estimate are wide, ranging from negative to positive estimates. This suggests that sampling error makes it difficult to estimate true temporal variability in the Southwest. The wide confidence intervals of the standard deviation reflect that uncertainty (Table 11). A positive temporal variance was estimated for the other two regions. In the Northwest 38.3% of the SE of the mean survival probability was due to sampling variance, compared to 52.9% on the Atlantic Coast, the region with the lowest annual sighting probability (Table 4).

Discussion

Adult Survival

The results of the GOF tests for three of the regions identified heterogeneity in capture or survival probabilities among individuals—a violation of an assumption

Table 8.   Comparison of fit for models of survival of adults in the Upper St. Johns River region.

Model[a]	# Parameters	ΔQAICc	QAICc weight
$\phi(\cdot)\ p(g)$	3	0.00	0.628
$\phi(g)\ p(g)$	4	1.05	0.372
$\phi(\cdot)\ p(g+t)$	22	19.04	<0.001
$\phi(\cdot)\ p(\cdot)$	2	20.12	<0.001
$\phi(g+t)\ p(g)$	20	30.46	<0.001
$\phi(t)\ p(g)$	24	34.41	<0.001
$\phi(g*t)\ p(g)$	44	67.62	<0.001
$\phi(g*t)\ p(\cdot)$	43	88.99	<0.001
$\phi(g*t)\ p(t)$	63	114.12	<0.001
$\phi(g*t)\ p(g*t)$	82	126.42	<0.001

[a] ϕ = survival probability, p = capture probability, symbols in ( ) indicate factors affecting variation, t = time, g = group, * indicates interaction, + indicates additive effect, $(\cdot)$ = no variation.

for capture-recapture analysis. Although sampling heterogeneity can contribute to the lack of fit, a major factor most likely is grounded in the biology of manatees in the colder northern portions of this species' natural range. During cold years most individuals will be driven into the aggregation sites with equal probability of sighting at least once in the season. During warm winters, however, physiological stress from cold is not severe. Some individuals habitually return each year to aggregation sites and are identified repeatedly during the season; others come in only during the coldest days or find short-term refuge in minor warm-water sites or deep water where we do not routinely monitor. Consequently capture probabilities vary among individuals and results in what is referred to in capture-recapture studies as non-random temporary emigration out of the study area (Kendall *et al.* 1997). The study area in the case of manatees is not the specific region where manatees range, but the small warm-water sites where manatees aggregate and are available for photo-documentation. An example of this phenomenon can be seen with the analysis for the Upper St. Johns River region. Despite the high annual capture probability (0.927), for a couple of years when cold came early to the state, a small number of males were photo-documented wintering at sites along the Atlantic coast (CAB unpublished). Apparently the early season did not allow them time to travel to Blue Spring and the small sample size resulted in a significant GOF test.

This heterogeneity, however, is not necessarily a fatal flaw to valid estimation of survival rates. Computer simulations (Carothers 1973) have demonstrated that survival estimates are robust to heterogeneity in capture probabilities, particularly when capture probabilities are as high as those in this study (Table 4) and if heterogeneity is the same each year. Using prescribed statistical procedures to inflate the variance provides an objective means of describing the uncertainty of the precision of the estimates. The importance to resource managers and researchers of realistic estimates of uncertainty has previously been highlighted for marine mammal studies (Ralls and Taylor 2000). The higher variance, however, reduces the power to differentiate among competing models that describe various patterns of variation and the factors thought to affect that variation; simpler models with fewer parameters are more easily fit to the data, particularly if sample size is small or sighting probabilities low.

Table 9. Comparison of fit for models of survival of adults on the Atlantic Coast region.

Model[a]	# Parameters	ΔQAICc	QAICc weight
ϕ(trend) $p(t)$	18	0.00	0.824
$\phi(\cdot)$ $p(t)$	17	3.11	0.174
$\phi(t)$ $p(t)$	30	11.86	0.002
$\phi(t)$ $p(\cdot)$	14	63.64	<0.001
$\phi(\cdot)$ $p(\cdot)$	2	78.50	<0.001

[a] ϕ = survival probability, p = capture probability, symbols in ( ) indicate factors affecting variation, t = time, $(\cdot)$ = no variation.

Nonetheless, ecological patterns were identified through the evaluation of competing models. By partitioning individuals into more homogenous groups within a region, through the modeling process, we successfully identified patterns of ecological variation and estimated survival rates specific to that variation and those groups, which informs researchers and resource managers about processes affecting manatee population dynamics. In the Northwest, an effect on survival from intense coastal storms, identified in a previous analysis with fewer years of data (Langtimm and Beck 2003), was supported. Survival probabilities during two of the storm years, 1993 and 1995, increased with this analysis, providing support for one possible mechanism for the effect—some individuals are displaced during the storm and can eventually find their way back. The Northwest modeling effort also suggests that the larger temporal variance estimated for the Northwest region is due at least in part to the occurrence of two of the three identified storms in the most recent 10-yr period. Natural rather than human-related factors may have the most influence on adult survival in the region, at least up to this point in time.

In the Upper St. Johns River, the high sighting probabilities for natives supports strong fidelity of members of this group to the winter aggregation site and is consistent with telemetry findings of natal philopatry to winter and summer ranges learned in the first few years of life (Deutsch *et al.* 2003). In contrast, capture probabilities were lower for the "immigrant group." The magnitude of the differences between the two groups in the point estimates of survival probabilities suggest there may be differences in behavior and consequently survival, which warrant further study. Immigrants probably range more widely, subject to different mortality risks. It might be argued that the immigrant group is older with an expected reduction in annual survival rate, but relatively constant survival over time once adult status is reached is a life history trait common to large mammals (Fowler 1981) and vertebrates in general (Charnov 1986). Rates of senescence are low in other mammals with life history traits similar to those of manatees: large body mass, lengthy gestation, and small litter size (Gaillard *et al.* 1994).

The negative time trend we found on the Atlantic Coast is cause for concern, but may be an artifact of temporary emigration by some manatees. Monitoring effort was reduced over the last three years in this region due to fewer manatees aggregating at the power plant effluents because of warmer than normal winters (1998–1999, 1999–2000, 2001–2002), coupled with limited resources to increase effort. This extended time period occurred at the end of the sighting histories and could have produced a spurious trend. Animals may be alive, but were not available for photographing. We attempted in a *post hoc* analysis to model some of the sighting heterogeneity with a robust design that models non-random temporary emigration of individuals from the monitoring site (Kendall *et al.* 1997; see

Table 10. Comparison of fit for models of survival of adults in the Southwest region.

Model[a]	# Parameters	ΔQAICc	QAICc weight
$\phi(\cdot)\ p(\cdot)$	2	0.00	0.471
$\phi(\cdot)\ p(g)$	3	1.70	0.201
$\phi(g)\ p(\cdot)$	3	1.85	0.187
$\phi(g)\ p(g)$	4	3.35	0.088
$\phi(g)\ p(g*t)$	16	6.24	0.021
$\phi(g*t)\ p(g+t)$	19	9.15	0.005
$\phi(t)\ p(\cdot)$	8	9.24	0.005
$\phi(g*t)\ p(g)$	16	9.61	0.004
$\phi(g*t)\ p(\cdot)$	15	9.69	0.004
$\phi(\cdot)\ p(g+t)$	9	10.70	0.002
$\phi(g+t)\ p(\cdot)$	9	10.82	0.002
$\phi(t)\ p(g)$	9	11.01	0.002
$\phi(t)\ p(g+t)$	14	11.43	0.002
$\phi(g+t)\ p(g)$	10	12.08	0.001
$\phi(g)\ p(g+t)$	22	12.22	0.001
$\phi(g*t)\ p(t)$	20	16.03	<0.001
$\phi(g*t)\ p(g*t)$	26	22.82	<0.001

[a] ϕ = survival probability, p = capture probability, symbols in ( ) indicate factors affecting variation, t = time, g = group, * indicates interaction, + indicates additive effect, ($\cdot$) = no variation.

discussion below). This class of models is available in Program MARK. The fit of the general model to the data was good, with a variance inflation factor of 1.3),[3] but the analysis was not conclusive with regard to trend. Additional years of data are needed to clarify the pattern in a future analysis.

In the Southwest we were not able to discern any patterns of variation in survival probabilities, despite the region experiencing unusual mortality events during the study from a red-tide bloom and a severe winter, and annual variation in the number of carcasses identified as human-related deaths. The model with annual variability in survival was not the highest ranked model (Table 10) and temporal variance was estimated at zero but with a wide 95% CI (Table 11), suggesting that sampling variation was large. The Southwest is the most difficult region in which to collect photo-identification data and the lowest water clarity in the state. There are fewer years of data and earlier efforts were uneven with more focus on some areas than others because of logistical constraints. Despite the difficult monitoring conditions, sighting probabilities estimated from the data were high at 66% (Table 4). We expect survival analysis in the region to improve in precision as the geographic coverage, sample size, and years of study increase.

Juvenile Survival

Estimates of age-specific survival through the immature stages are often lacking for marine mammal species (Eberhardt and Siniff 1977) and other large mammals and most frequently are based on age-at-death life tables that assume stable populations and do not allow analysis of variability (Gaillard *et al.* 1993). The age-specific estimates of calf and subadult survival rates presented here for the Upper

[3] Personal communication from William Kendall, USGS Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, Maryland 20708, U.S.A., 26 February 2003.

Table 11. Mean annual survival rates for the most recent 10-year period and estimated process variation.

Region	Years[a]	Model	$\hat{c}$	Mean survival probability (SE)	Temporal variance (σ^2) (95% CI)	Standard deviation (σ) (95% CI)
Northwest	1990–1999	ϕ_t/t_t	1.00	0.956 (0.007)	0.00017 (−0.00013–0.00283)	0.0129 (0.00000–0.053278)
Upper St. Johns River[b]	1990–1999	ϕ_t/t_g	2.37	0.960 (0.011)	−0.00077 (−0.00077–−0.00044)	0.0000 (0.0000–0.0000)
Atlantic Coast	1990–1999	ϕ_t/t_t	1.95	0.937 (0.008)	0.00014 (−0.00034–0.00273)	0.0118 (0.0000–0.0522)
Southwest[c]	1995–2000	ϕ_t/t_g	2.67	0.908 (0.019)	−0.00142 (−0.00161–0.00830)	0.0000 (0.0000–0.0911)

[a] Data from all available years were used to estimate annual survival and variance, however mean survival probability and variance were calculated only from the estimates for the listed years. Estimates before the time span listed were excluded from the mean.

[b] Subadults and adults included in analysis.

[c] Estimates only available for six years.

St. Johns River are the first estimates for the Florida manatee based on capture-recapture statistical models. Data are currently not adequate for the other regions. As expected, survival rates were lowest for 1st- and 2nd-yr calves, but survival dramatically improved after yr 1, when some, but not all calves, are weaned. There is considerable individual and regional variation in length of calf dependency (1–2 yr); after yr 2, all calves are independent. In yr 3–4, many individuals are pre-reproductive (Hernandez *et al.* 1995, Marmontel 1995, O'Shea and Hartley 1995, Rathbun *et al.* 1995), but survival probabilities approached those of prime-age adults. No differences were detected between adults (>5 yr) and subadults (3, 4, and 5 yr). Sample sizes were small, however, and with a larger data set it may be possible to differentiate among these age-classes. This analysis, however, suggests that the period of calf dependency and weaning is the most vulnerable stage of a manatee's life.

Juvenile survival probabilities of large mammals in general are more sensitive to environmental variation than adult survival (Eberhardt 1977, Benton and Grant 1996) and can show high annual fluctuations (Gaillard *et al.* 1998). Unfortunately, sample sizes were not large enough to detect patterns of annual variation. Closer scrutiny and analysis is warranted, if better methods can be found to mark and monitor young.

Comparisons Among Regions

Direct estimates of age-specific calf and subadult survival rates are only available for the Upper St. Johns River. The use of estimates from this region as surrogates for estimates in other regions should be done with caution. Juvenile survival rates most likely are not comparable among regions. Calves are usually weaned after one year in the Upper St. Johns River (O'Shea and Hartley 1995), whereas calves are usually dependent for two years in the Northwest (Rathbun *et al.* 1995). Adult survival was higher in the Upper St. Johns River than in the Atlantic Coast and Southwest, and may be higher for juveniles as well. Deaths from cold stress affect calves and subadults more frequently than adults (Buergelt *et al.* 1984). However deaths from cold stress are low in the Upper St. Johns River.

Mean annual adult survival probabilities for the most recent 10-yr time period differed among the management regions (Table 11). All survival rates were high and were consistent with life-history theory and the high probabilities estimated for other large mammals (Buckland 1990, Amstrup and Durner 1995). The lowest survival, however, was estimated for the Atlantic Coast and Southwest, the two regions with the greatest human development, the largest proportion of watercraft-related deaths (Ackerman *et al.* 1995), and where manatees find winter refuge at industrial warm-water effluents. The Northwest and Upper St. Johns River regions are less impacted by humans, manatees over-winter at natural warm-water sites, and there are strong management efforts to protect these winter sites.

Comparison of the status of the populations in these regions, however, requires placing adult and juvenile survival into a larger context through the integration of survival estimates, other vital rates, and demographic parameters into a model of manatee population dynamics. The estimates presented here were specifically undertaken for a newly developed stage-based population model (see Runge *et al.* 2004).

The methods we used are statistically robust (Lebreton *et al.* 1992, Williams *et al.* 2001), and provide the best estimates of survival probabilities and precision for each of the regions. It should be noted, however, that the precision and certainty

of these estimates, vary among regions due to differences in the results of the GOF test and magnitude of the variance inflation factor (Table 3), the length of the time-series for monitoring, and possible sources of bias. The lowest estimates are for the Southwest, the region with the highest variance inflation factor, a negative estimate of temporal variance indicating large sample error, and the shortest time-series (8 yr). Effects from non-random temporary emigration and possible permanent emigration of individuals out of the region could result in a spurious lower apparent survival. Greater scrutiny of the data for movement of individuals between the Northwest and Southwest regions are planned by the MIPS database managers, but have not yet been completed. Individuals also may have migrated to south Florida and the area of Ten Thousand Islands National Wildlife Refuge and Everglades National Park, where we currently lack a monitoring effort due to logistical constraints and poor conditions for effective photography. But bias due to permanent emigration is probably low, as manatees show high fidelity to wintering sites (Reid *et al.* 1991, O'Shea and Hartley 1995, Rathbun *et al.* 1995, Deutsch *et al.* 2003). Lack of photo-identification data from the Everglades area, however, limits estimation for the Southwest to a smaller pool of individuals that excludes manatees resident to the most southern portion of the region, possibly biasing the regional estimates. Further data collection and analysis are needed to adequately assess this region.

Error in Identification due to Changes in Natural Marks

Survival estimates can be biased if marks to identify individuals are lost or change. The marks on manatees are dynamic. Individuals can acquire new scars from collisions with watercraft confounding the appearance of the original identifying mark and raising questions about errors in identification. New scars however, in the majority of cases do not obliterate information. New scar patterns can be laid down on top of old patterns, but watercraft hulls and propellers that cause injuries frequently produce a characteristic large scar pattern consisting of multiple distinct elements distributed across the body or tail (Fig. 2). In some cases it is possible to determine the type of boat and direction of approach by analysis of the pattern (Beck *et al.* 1982, Wright *et al.* 1995). Because of the spacing among elements, a second injury on top of the first may obliterate some parts of the original pattern, but some elements remain with distinctive features for matching. There is redundant information within a single scar pattern, which helps ensure that an identifying mark will not be totally lost. Experienced personnel are skilled in identifying and visually isolating patterns from a single watercraft encounter and using the elements within the pattern to make matches. Furthermore, nearly all individuals in the catalog have multiple scars patterns distributed over more than one part of the body, again providing additional information to verify matches. Misidentifications still can occur, but we believe the rate of error is low because of the conservative and stringent protocols for cataloging individuals, accepting data, and verifying matches (see Methods). Bias should be minimal and any errors would result in the loss of a mark (*i.e.*, loss of identity of the animal) and an underestimation of apparent survival probability (Arnason and Mills 1981), a conservative interpretation for this endangered species.

Other methods of marking have been tested with manatees. Freeze brands fade and only are used for short-term monitoring, such as of released captives. Currently animals captured for telemetry studies or rescued for rehabilitation routinely are

injected with a passive integrated transponder (PIT) tag, which can be electronically scanned for an identification number (Wright *et al.* 1998). However, to provide adequate data for estimates of survival, hundreds of animals would need to be captured and tagged each year. Captures require large teams of people; are expensive, time consuming, and are not without danger to animal and researcher. Deaths of animals during capture are rare, but have occurred (Deutsch *et al.* 2003). To date, scars, natural marks, and photo-identification provide the best means to monitor individuals and estimate adult life-history parameters. We have years of data, the technique is non-intrusive, and does not influence an individual's survival or resighting probability, as sometimes can occur when an animal is captured and marked. Monitoring calves and subadults, however, remains problematic and new methods of marking are needed to provide life-history parameters for these important age classes.

Recommendations to Improve Monitoring and Estimates

The results of this analysis were presented at the Manatee Population Ecology and Management Workshop held in April 2002 in Gainesville, Florida. A review panel at the session outlined several recommendations to specifically improve analysis of manatee survival estimates, but which apply in general to the design of any capture-recapture study (Pollock *et al.* 1990:68–71, Williams *et al.* 2001). Some of the recommendations will be implemented for future analyses; others were incorporated into the analyses presented here: (1) Reduce heterogeneity in sampling. Increase field effort to provide better geographic coverage and consistent within-season sampling. Efforts should be made to ensure that all sections of the study area are sampled with equal intensity. (2) Stratify the sample of individuals for separate analysis. Grouping data into cohorts of individuals suspected to share common survival and sighting probabilities reduces heterogeneity, allows the simultaneous modeling of multiple groups, and permits an analysis of variance approach to test for differences among groups (Lebreton *et al.* 1992). If individuals can change strata, applications are available to model transition probabilities. The use of multi-state models (Hestbeck *et al.* 1991, Brownie *et al.* 1993) allows for the estimation of transition probabilities among strata or movement probabilities among locations and the estimation of survival probabilities associated with the transition. (3) Identify sources of heterogeneity and model the heterogeneity. The component GOF tests in Program RELEASE can supply information on sources of heterogeneity and capture-recapture applications are available to model different types of heterogeneity. A primary concern for manatee models is non-random temporary emigration away from the winter monitoring sites during years with warmer weather. This effect can be modeled (Kendall *et al.* 1997) with Pollock's robust design (Pollock 1982). The approach entails dividing each sampling period into at least two separate sessions and using this additional within-season information to estimate probabilities of temporary emigration and to estimate demographic parameters in the presence of temporary emigration. (4) Incorporate carcass recovery of known individuals into survival models with the Barker model. With the effort to match carcasses to individuals in the MIPS database, it is possible to model survival probabilities using both live sightings and dead recoveries of cataloged individuals (Barker 1997). An additional advantage of the Barker model is that it incorporates all live sightings of individuals, not just those during the formal winter sample interval. Thus with the dead recovery data it can provide

estimates of cause-specific (*e.g.*, watercraft-related) mortality, excluding permanent emigration. (5) Expand research beyond retrospective analysis to identify patterns of variation. Targeted research should be designed to study the processes affecting variation in survival, particularly with regard to questions of the effectiveness of management actions.

The manatee-sighting database is dynamic and growing and will continue to be an important source of information to researchers and managers. With the development of new capture-recapture statistical approaches to better estimate population parameters (Kendall *et al.* 2003, 2004), and development of new models for population dynamics (Runge *et al.* 2004), we look forward to new insights and new advances in our understanding of manatee population biology.

Literature Cited

ACKERMAN, B. B. 1995. Aerial surveys of manatees: A summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

ACKERMAN, B. B., S. D. WRIGHT, R. K. BONDE, D. K. ODELL AND D. J. BANOWETZ. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–258 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

ANDERSON, D. R., K. P. BURNHAM AND G. C. WHITE. 1994. AIC model selection in over-dispersed capture-recapture data. Ecology 75:1780–1793.

ANDERSON, D. R., K. P. BURNHAM AND G. C. WHITE. 1998. Comparison of AIC and CAIC for model selection and statistical inference from capture-recapture studies. Journal of Applied Statistics 25:263–282.

ARMSTRUP, S. C., AND G. M. DURNER. 1995. Survival rates of radio collared female polar bears and their dependent young. Canadian Journal of Zoology 73:1312–1322.

ARNASON, A. N., AND K. H. MILLS. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences 38:1077–1095.

BARKER, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. Biometrics 53:666–677.

BECK, C. A., R. K. BONDE AND G. B. RATHBUN. 1982. Analyses of propeller wounds on manatees in Florida. Journal of Wildlife Management 46:531–535.

BECK, C. A., AND J. P. REID. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman

and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

BENGTSON, J. L. 1981. Ecology of manatees (*Trichechus manatus*) in the St. Johns River, Florida. Ph.D. Dissertation, University of Minnesota, Minneapolis, MN. 126 pp.

BENTON, T. G., AND A. GRANT. 1996. How to keep fit in the real world: elasticity analysis and selection pressures on life histories in a variable environment. The American Naturalist 147:115–139.

BOSSART, G. D., D. G. BADEN, R. Y. EWING, B. ROBERTS AND S. D. WRIGHT. 1998. Brevetoxicosis in manatees (*Trichechus manatus latirostris*) from the 1996 epizootic: Gross, histologic, and immunohistochemical features. Toxicologic Pathology 26:276–282.

BOYCE, M. S. 2001. Population viability analysis: Development, interpretation, and application. Pages 123–136 *in* T. M. Shenk and A. B. Franklin, eds. Modeling in natural resource management: Development, interpretation, and application. Island Press. Washington, DC.

BROWNIE, C., J. E. HINES, J. D. NICHOLS, K. H. POLLOCK AND J. B. HESTBECK. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173–1187.

BUCKLAND, S. T. 1990. Estimation of survival rates from sightings of individually identifiable whales. Report of the International Whaling Commission (Special Issue 12):149–153.

BUERGELT, C. D., R. K. BONDE, C. A. BECK AND T. J. O'SHEA. 1984. Pathologic findings in manatees in Florida. Journal of the American Veterinary Medical Association 185:1331–1334.

BURNHAM, K. P., AND D. R. ANDERSON. 1998. Model selection and inference: A practical information-theoretic approach. Springer-Verlag, New York, NY.

BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5:1–437.

CAROTHERS, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

CASWELL, H., M. FUJIWARA AND S. BRAULT. 1999. Declining survival probability threatens the North Atlantic right whale. Proceedings of the National Academy of Sciences, USA 96:3308–3313.

CHARNOV, E. L. 1986. Life history evolution in a "recruitment population": Why are adult mortality rates constant? Oikos 47:129–134.

DEUTSCH, C. J., J. P. REID, R. K. BONDE, D. E. EASTON, H. I. KOCHMAN AND T. J. O'SHEA. 2003. Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic Coast of the United States. Wildlife Monographs 151:1–77.

EBERHARDT, L. L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environmental Conservation 4:205–212.

EBERHARDT, L. L. 1985. Assessing the dynamics of wild populations. Journal of Wildlife Management 49:997–1012.

EBERHARDT, L. L., AND T. J. O'SHEA. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

EBERHARDT, L. L., AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183–190.

FOWLER, C. W. 1981. Comparative population dynamics in large mammals. Pages 437–455 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York, NY.

FUJIWARA, M., AND H. CASWELL. 2001. Demography of the endangered North Atlantic right whale. Nature 414:537–541.

GAILLARD, J.-M., D. DELORME, J.-M. BOUTIN, G. VAN LAERE, B. BOISAUBERT AND R. PRADEL. 1993. Roe deer survival patterns: A comparative analysis of contrasting populations. Journal of Animal Ecology 62:778–791.

GAILLARD, J.-M., D. ALLAINE, D. PONTIER, N. G. YOCCOZ AND D. E. L. PROMISLOW. 1994. Senescence in natural populations of mammals: A reanalysis. Evolution 48:509–516.

GAILLARD, J.-M., M. FESTA-BIANCHET AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58–63.

GARCIA-RODRIGUEZ, A. I. 2000. Genetic studies of the West Indian manatee (*Trichechus manatus*). Ph.D. thesis, University of Florida, Gainesville, FL. 115 pp.

GOULD, W. R., AND J. D. NICHOLS. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79:2531–2538.

HAMMOND, P. S., S. A. MIZROCH AND G. P. DONOVAN, EDS. 1990. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission (Special Issue 12).

HARGROVE, J. W., AND C. H. BORLAND. 1994. Pooled population parameter estimates from mark-recapture data. Biometrics 50:1129–1141.

HARTMAN, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication 5:1–153.

HERNANDEZ, P., J. E. REYNOLDS, III, H. MARSH AND M. MARMONTEL. 1995. Age and seasonality in spermatogenesis of Florida manatees. Pages 84–97 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

HESTBECK, J. B., J. D. NICHOLS AND R. A. MALECKI. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–533.

KENDALL, W. L., J. E. HINES AND J. D. NICHOLS. 2003. Adjusting multistate capture-recapture models for misclassification bias: manatee breeding proportions. Ecology 84:1058–1066.

KENDALL, W. L., C. A. LANGTIMM, C. A. BECK AND M. C. RUNGE. 2004. Capture-recapture analysis for estimating manatee reproductive rates. Marine Mammal Science 20: 424–437.

KENDALL, W. L., J. D. NICHOLS AND J. E. HINES. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563–578.

LANGTIMM, C. A., AND C. A. BECK. 2003. Lower survival probabilities for adult Florida manatees in years with intense coastal storms. Ecological Applications 13:257–268.

LANGTIMM, C. A., T. J. O'SHEA, R. PRADEL AND C. A. BECK. 1998. Estimates of annual survival probabilities for adult Florida manatees (*Trichechus manatus latirostris*). Ecology 79:981–997.

LEBRETON, J.-D., K. P. BURNHAM, J. CLOBERT AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62:67–118.

LEFEBVRE, L. W., B. B. ACKERMAN, K. M. PORTIER AND K. H. POLLOCK. 1995. Aerial survey as a technique for estimating trends in manatee population size—problems and prospects. Pages 63–74 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

LINK, W. A., AND J. D. NICHOLS. 1994. On the importance of sampling variance to investigations of temporal variation in animal population size. Oikos 69:539–544.

MARMONTEL, M. 1995. Age and reproduction in female Florida manatees. Pages 98–119 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

O'SHEA, T. J., AND W. C. HARTLEY. 1995. Reproduction and early-age survival of manatees at Blue Spring, Upper St. Johns River, Florida. Pages 157–170 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

O'SHEA, T. J., AND C. A. LANGTIMM. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

O'SHEA, T. J., C. A. BECK, R. K. BONDE, H. I. KOCHMAN AND D. K. ODELL. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management 49:1–11.

O'SHEA, T. J., G. B. RATHBUN, R. K. BONDE, C. D. BUERGELT AND D. K. ODELL. 1991. An epizootic of Florida manatees associated with a dinoflagellate bloom. Marine Mammal Science 7:165–179.

POLLOCK, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:757–760.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1–97.

RALLS, K., AND B. L. TAYLOR. 2000. Special section: Better policy and management decisions through explicit analysis of uncertainty: New approaches from marine conservation. Conservation Biology 14:1240–1242.

RATHBUN, G. B., J. P. REID AND G. CAROWAN. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publication 48:1–33.

RATHBUN, G. B., J. P. REID, R. K. BONDE AND J. A. POWELL. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

REID, J. P., G. B. RATHBUN AND J. R. WILCOX. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science 7:180–190.

REYNOLDS, J. E., III, AND J. R. WILCOX. 1994. Observations of Florida manatees (*Trichechus manatus latirostris*) around selected power plants in winter. Marine Mammal Science 10:163–177.

RUNGE, M. C., C. A. LANGTIMM AND W. L. KENDALL. 2004. A stage-based model of manatee population dynamics. Marine Mammal Science 20:361–385.

SHANE, S. H., AND D. MCSWEENEY. 1990. Using photo-identification to study pilot whale social organization. Report of the International Whaling Commission (Special Issue 12):259–263.

U.S. FISH AND WILDLIFE SERVICE [USFWS]. 2001. Florida manatee recovery plan, (*Trichechus manatus latirostris*), third revision. U.S. Fish and Wildlife Service, Atlanta, GA. 138 pp.

U.S. FISH AND WILDLIFE SERVICE [USFWS]. 2002. Florida manatees; incidental take during specified activities. Federal Register 67:69078–69104.

WEIGLE, B. L., I. E. WRIGHT, M. ROSS AND R. FLAMM. 2001. Movements of radio-tagged manatees in Tampa Bay and along Florida's west coast, 1991–1996. Florida Marine Research Institute Technical Reports TR-7. St. Petersburg, FL. 156 pp.

WELLS, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199–225 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Methods of study. University of California Press, Berkeley, CA.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.

WHITE, G. C., K. P. BURNHAM AND D. R. ANDERSON. 2001. Advanced features of Program MARK. Pages 368–377 *in* R. Field, R. J. Warren, H. Okarma and P. R. Seivert, eds. Wildlife, land, and people: Priorities for the 21st Century. Proceedings of the Second International Wildlife Management Congress. The Wildlife Society, Bethesda, MD.

WILLIAMS, J. M., AND I. W. DUEDALL. 1997. Florida hurricanes and tropical storms. University Press of Florida, Gainesville, FL.

WILLIAMS, B. K., J. D. NICHOLS AND M. J. CONROY. 2001. Analysis and management of animal populations: Modeling, estimation, and decision making. Academic Press, San Diego, CA.

WRIGHT, S. D., B. B. ACKERMAN, R. K. BONDE, C. A. BECK AND D. J. BANOWETZ. 1995. Analysis of watercraft-related mortality of manatees in Florida, 1979–1991. Pages 259–268 *in* T. J. O'Shea, B. B. Ackerman and H. F. Percival, eds. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report 1.

WRIGHT, I. E., S. D. WRIGHT AND J. M. SWEAT. 1998. The use of passive integrated transponder (PIT) tags in identifying manatees (*Trichechus manatus latirostris*). Marine Mammal Science 14:641–645.

WÜRSIG, B., F. CIPRIANO AND M. WÜRSIG. 1991. Dolphin movement patterns: information from radio and theodolite tracking studies. Pages 79–111 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Methods of study. University of California Press, Berkeley, CA.

ZEH, J., D. POOLE, G. MILLER, W. KOSKI, L. BARAFF AND D. RUGH. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981–1998 photoidentification data. Biometrics 58:832–840.